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Decomposition of Organic Matter in Tundra

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SUMMARY

Data on dry weight losses from plant material in tundra sites are examined in relation to decomposition processes and organic matter accumulation, as influenced by various environmental factors and by substrate "quality":

1. Graphical analysis indicates that decay rates of litter vary with species, site, age of the litter and its position in the soil profile. No clear seasonal patterns are observable, being largely confused and obscured by short-term fluctuations and a high initial loss, probably due to leaching.

2. Variation with time and depth in the soil are eliminated by selection of data on first year percentage losses in or on the litter layer. Data on loss rates of 62 litters in 23 sites are tested for differences between site and litter classes. Mosses, Lichens and Woody litters have lower loss rates than Shrub shoots and "Hard" Leaves (e.g. pine needles), which in turn have lower loss rates than "Soft" Leaves (e.g. *Rubus chamaemorus*). Decay rates are higher in Warm Oceanic sites than in sites with other types of temperature pattern. Mesic sites have higher rates than Wet or Dry sites, and pH and vegetation classes also show significant differences in decay rates.

3. Because of the interdependence of many environmental effects, the litter losses are also examined in relation to the principal component analysis of the Site Classification (French, this volume) and regressions are calculated on specific site factors. Climate becomes progressively more important relative to soil conditions as limitation due to litter quality is removed. Optimum moisture levels for decomposition are calculated to be around 400% of soil dry weight, and at these moisture levels, and average tundra levels of soil nutrients, decay rates increase linearly by about 20% per 1000° days above 0°C. Soil nutrient effects are less clearly definable.

4. These conclusions are partially corroborated by reference to an independent data set, where less detailed site data were available.

5. Data on standing dead and roots are very sparse. They appear to have similar decay rates to those of surface litters of similar quality, but no further general conclusions can be drawn.

6. The initial decay rates are modified as litter ages and moves further down the soil profile. Decay rates decline with age, especially in "soft" litters, and may also decline with depth in the soil, particularly under waterlogged conditions, leading to accumulation of peat. Estimates of the decay constant k (Jenny, Gessel & Bingham, 1949) derived from litter bag measurements and from measurements of production and accumulation are contrasted, and the reasons for the observed differences discussed. Finally, the use of constant-coefficient models of production, decay and accumulation in the elucidation of organic matter accumulation mechanisms is indicated.

INTRODUCTION

In tundra, most of the annual primary production is not consumed by herbivores, but dies and passes into the decomposition cycle. The type of soil which develops on a site is affected by the decay rates of the organic matter and this, together with the rates of release of nutrients from organic matter, affects subsequent plant growth. Decomposition is thus an important part of ecosystem functioning in the tundra.

The decomposition cycle can be visualized, as in the ABISKO model (Bunnell & Dowding, this volume), as a series of compartments (standing dead, litter, roots), with various transfers corresponding to the action of decomposition and other processes on the compartments. Each compartment contains the remains of a number of plant species, hence a complex assemblage of organic substrates and inorganic elements. The inputs to, and contents of, the compartments vary, but the decomposition processes and the factors controlling them are essentially the same in all compartments, differences between compartments being mainly a result of the relative importance of the various processes and parameters.

There are three main decomposition processes: release of carbon in gaseous form by microflora and fauna (respiration), leaching of soluble material, and comminution by fauna and physical factors. Transfers of material also occur through assimilation and growth by microflora and fauna, and physical removal and addition of material by fauna or frost action.

A widely used approach to the study of decomposition is the measurement of dry weight losses from plant material, particularly using litter bag methods (Bocock & Gilbert, 1957). The data used in this paper are dry weight losses of plant remains in litter and, to a lesser extent, standing dead and roots. Weight losses result from a combination of some or all of the processes described above and are thus an integration of a number of transfers in the ABISKO model. They are also integrated over months or years in the field, and therefore can be used to examine only broad correlations with environmental variables. This contrasts with the more sensitive short-term measurement of respiration, used to define causal relationships between decomposition and climate (Flanagan & Veum, this volume).

In this paper, the results from weight loss studies are examined, with the aims of:

1. Defining the rates of decomposition of plant remains in tundra
2. Showing the main sources of variation in decay rates
3. Examining a) the correlation of decomposition with environmental factors and substrate "quality" and b) the extent to which these factors account for the observed variation
4. Assessing the relationship between observed rates and patterns of decomposition and organic matter accumulation and turnover.

Detailed descriptions of methods and interpretation of results within a site are the responsibility of the individual site workers and will be published elsewhere.

Most of the data used herein are unpublished, or scattered through various reports and publications. The results are therefore given in detail and sources are gratefully acknowledged.

FIELD METHODS

The weight losses used in this paper have been measured by two main methods:

1. *Litter bags*. A known weight of material (usually about 1-10 g) is weighed, placed in a net bag, left in the field for a given period, then retrieved and reweighed. Most workers have used bags with medium-large mesh size (about 1 mm). Some litters in

The Hardangervidda sites were in small mesh bags (0.06 mm), and most Moor House and Macquarie Island litters were in hairnets or very large mesh bags (about 1 cm). In some cases, particularly for woody stems, the litters were simply tied to a nylon thread.

2. *Specific weight.* Litter bag measurements do not distinguish between weight loss resulting from decomposition and weight loss resulting from physical removal. To allow for removal, the weight per unit length, or area, of leaves and rhizomes of known age has been measured in some sites. This method has been used mainly for standing dead material.

SITES

Information on climatic and soil conditions at most of the sites where decomposition experiments were carried out is given in the papers on site classification (French, this volume) and soils (Brown & Veum, this volume). Some of the sites from which decomposition data were available were not included in the site classification paper. Most of these are described in the discussion of first litter losses, later in this paper. The remainder are briefly described here.

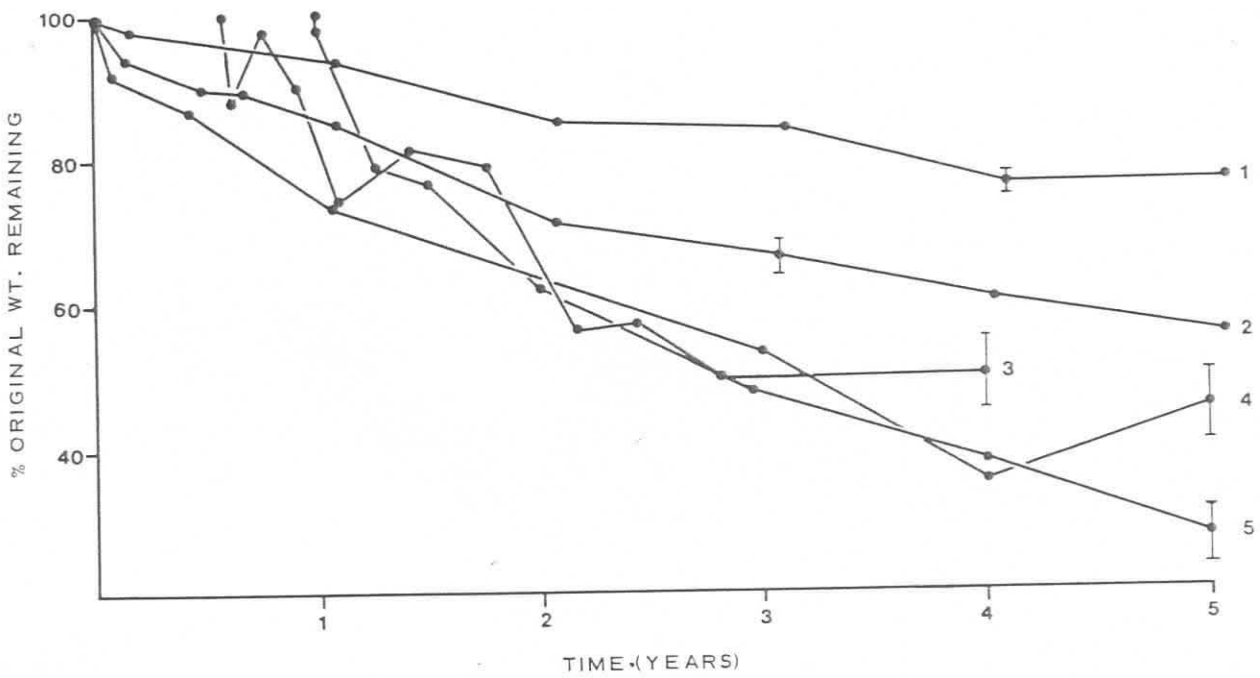
1. *Macquarie Island, Site M1.* This is a *Poa* grassland site, similar to M6B (see French, this volume), but with a more sandy soil.
2. *Signy Island, Chorisodontium.* A moss bank on the northwest coast of the island, similar to Hut Bank but deeper, more acid peat.
3. *Signy Island, Drepanocladus.* In the region of the Marble Knolls site, moss carpets with melt streams. Alkaline, eutrophic soil conditions.
4. *South Georgia* *Festuca* grassland with cryptogams on a relatively nutrient-rich mineral soil. Cold Oceanic climate.
5. *Eagle Summit.* Alpine heath in central Alaska.

RESULTS AND ANALYSES

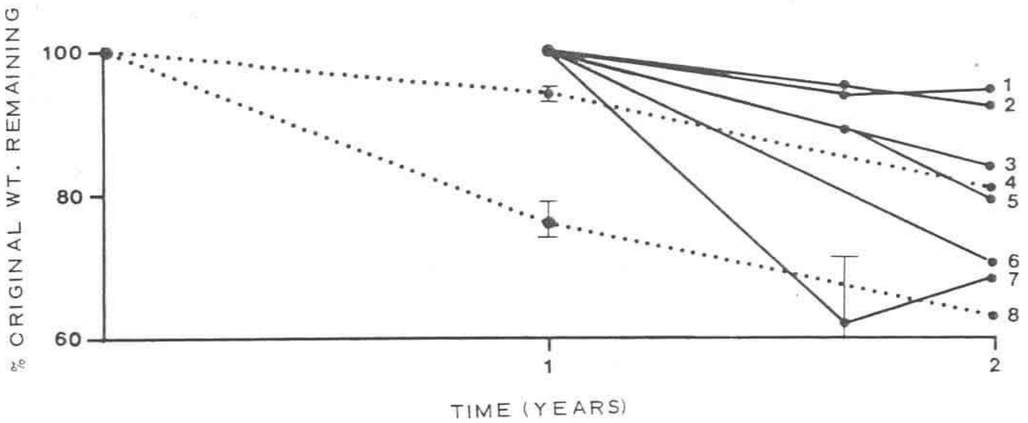
Review of Data on Litter Losses

The results are presented in Fig. 1 and 2 as graphs of the percentage of the original weight remaining, with time and depth. Visual comparison of these results indicates that:

1. There is considerable variation in the loss rates of different litters at the same site.
2. There are differences in the losses from comparable litters at different sites. For example, *Rubus chamaemorus* leaves lost 16-24% in the first year at Abisko (Fig. 1 b), 36-38% at Moor House (Fig 1 a and d) and 59% at Petchora (Gusinoe aapafen, not shown). First year losses of barley straw at the five Norwegian sites ranged from 10% at the Lichen Heath to 38-40% in the Birch Forest (Fig. 1 e- i).
3. In most cases, the shape of the curve indicates that the percentage of the original litter lost per unit time (absolute loss rate) declines with time. This declining absolute loss rate may result from a decline in a) the quality of the substrate, b) the rate of leaching and/or c) the efficiency of the decomposer organisms. Jenny, Gessel & Bingham (1949) have suggested that the fraction remaining as a function of time conforms to a negative exponential curve, i.e. that the fraction lost per unit time (proportional loss rate) is constant. Minderman (1968), Bunnell & Tait (this volume) and Van Cleve (this volume) have elaborated on this by suggesting that a truer model would be given by summation of a number of

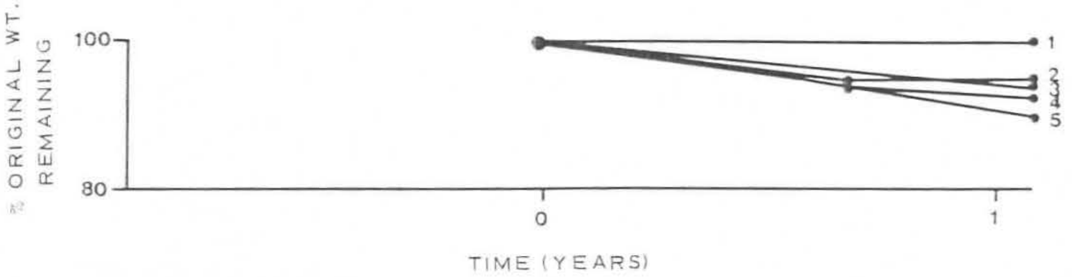


a. Moor House, October 1966-71 and 1963-66 (Juncus). *1:* Calluna *stems (on strings); 2:* Calluna *shoots (in bags); 4:* Eriophorum vaginatum *leaves; 5:* Rubus chamaemorus *leaves (1, 2, 4, 5 all on blanket bog); 3:* Juncus squarrosus *leaves (in bags on peaty podsol).*

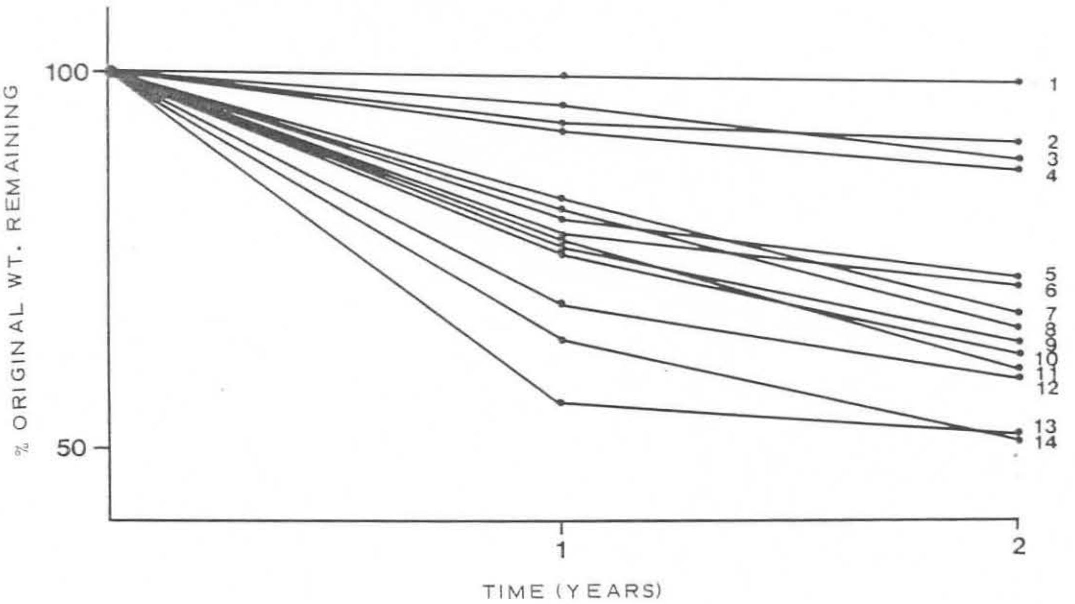


b. Abisko, Stordalen Mire, September 1970-72. 1: Andromeda polifolia *(aerial parts); 2:* Betula nana *twigs (on strings); 5:* Betula *leaves (wet); 6:* Betula *leaves (dry); 4:* Empetrum hermaphroditum *(aerial parts); 3, 8:* Rubus chamaemorus *leaves (in bags); 7:* Rubus *leaves (on strings).*

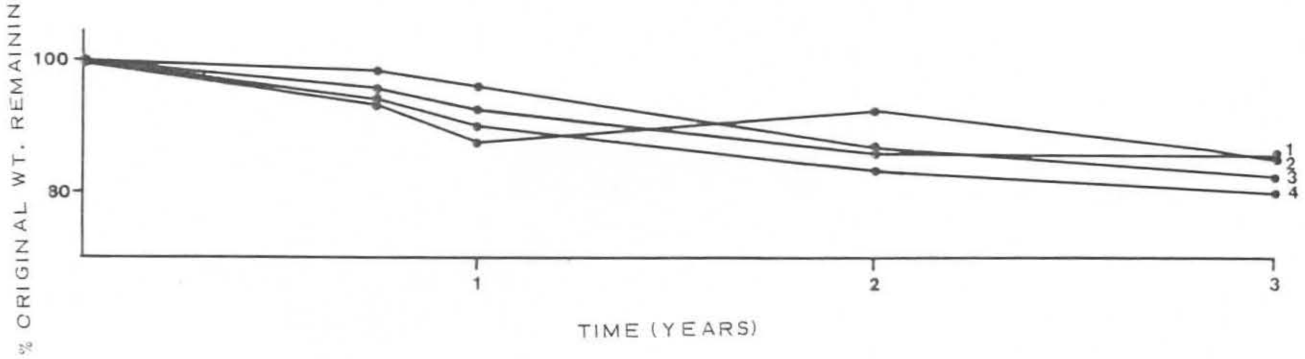
Fig. 1. Percentage of the original litter weight remaining plotted against time, in years, for various tundra sites. Litters were usually in bags with mesh size 0.5-1.0 mm, except at Hardangervidda, where some litters were in small mesh bags (0.06 mm) and at Moor House and Macquarie Island, where nets (about 1.0 cm) were used for most litters. Samples were placed on the litter surface except at Hardangervidda, where most litters were placed in or just below the litter layer. The scale of the graphs is variable.



c. Abisko, Stordalen Mire, August 1971-72. 1: Sphagnum fuscum; *2:* S. balticum; *3:* S. recurvum; *4:* S. riparium; *5:* S. lindbergii.

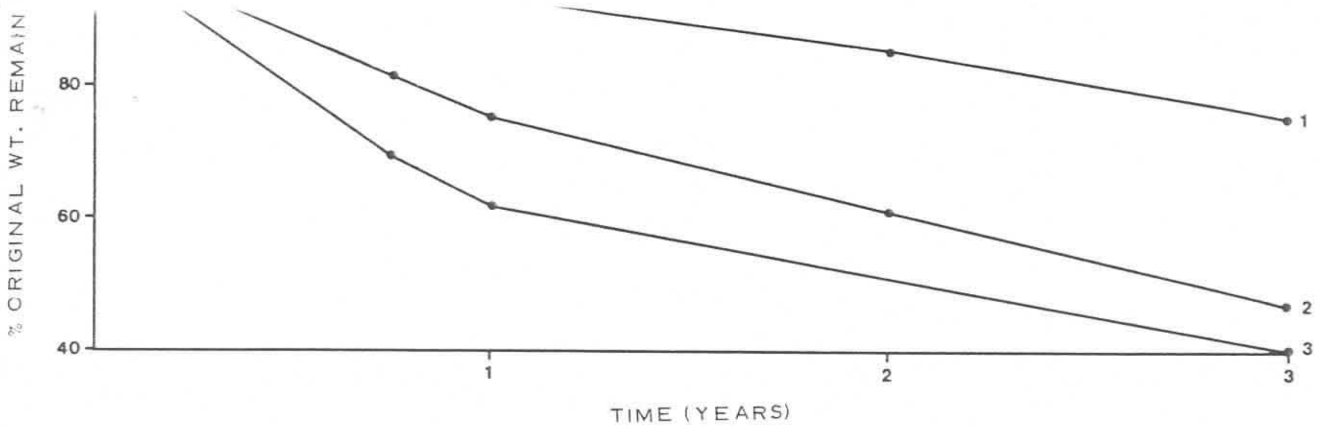


d. Moor House, October 1970-72. 1: Eriophorum vaginatum *roots; 2, 4:* Calluna *stems (on strings); 3:* Calluna *roots; 5:* Calluna *shoots (in bags); 6:* E. vaginatum *leaves; 7:* E. angustifolium *leaves (in bags); 8:* Trichophorum caespitosum *leaves; 9:* E. angustifolium *leaves (in nets); 10:* Pinus contorta *needles; 11:* Nardus stricta *leaves; 12:* Juncus effusus *leaves; 13:* Narthecium ossifragum *leaves; 14:* Rubus chamaemorus *leaves.*

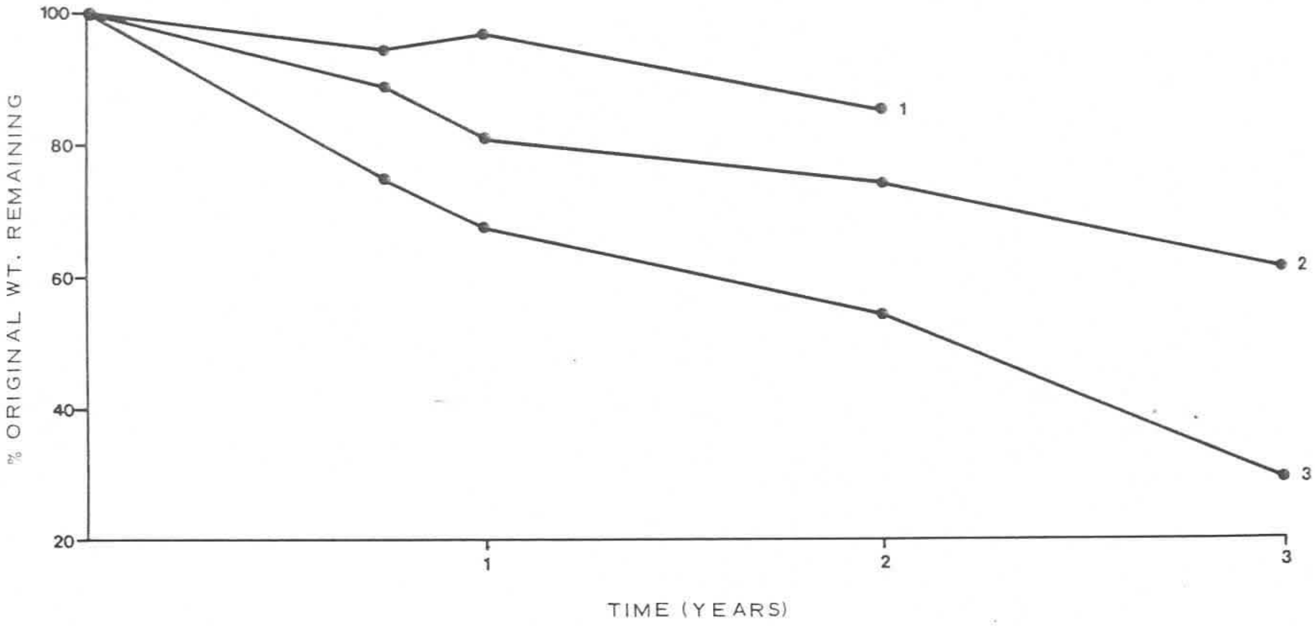


e. Hardangervidda, Lichen Heath, September 1969-72. 1: Lichens (small mesh bags); 2: Mixed site litter, vascular plants; 3: Lichens; 4: Barley straw.

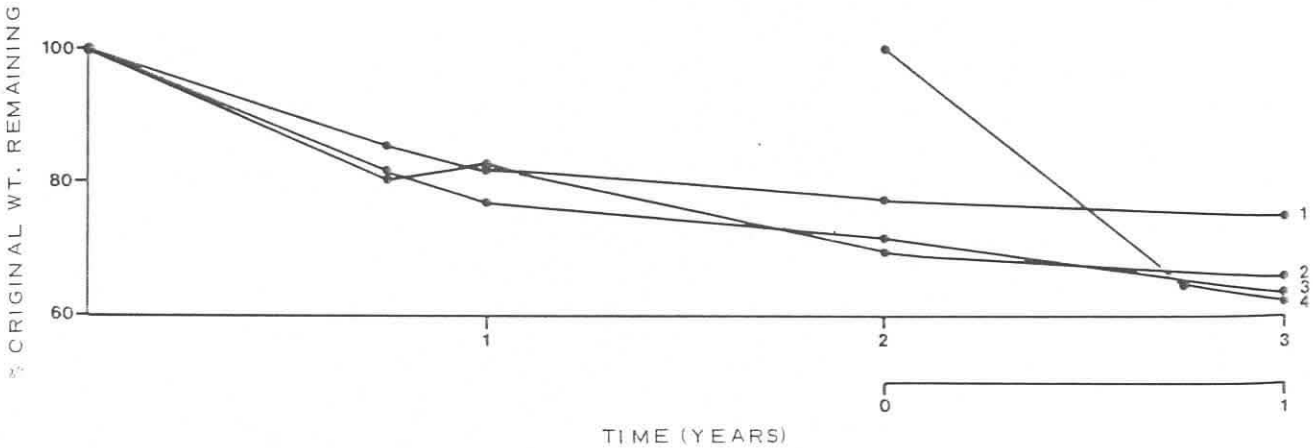
Fig. 1 (Cont'd).



f. Hardangervidda, Dry Meadow, September 1969-72. 1: Dryas octopetala; *2: Barley straw; 3: Mixed site litter, except* Dryas.

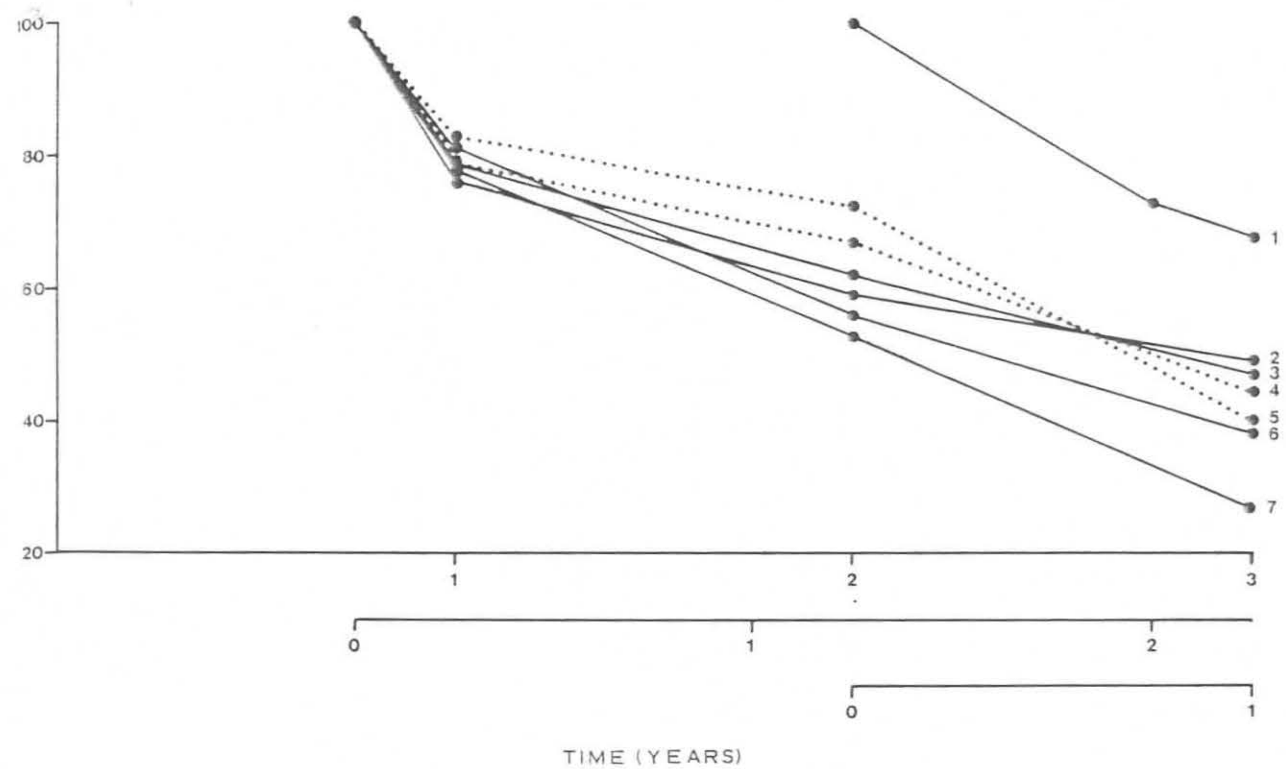


g. Hardangervidda, Wet Meadow, September 1969-72. 1: Mixed mosses; 2: Barley straw; 3: Mixed site litter, vascular plants.

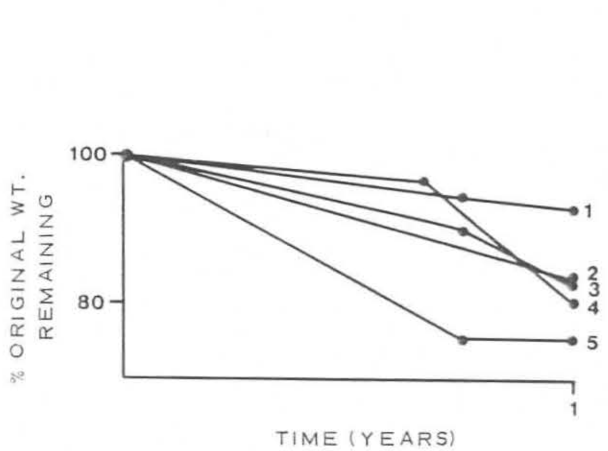


h. Hardangervidda, Snowbed, September 1969-72. 1: Mixed site litter, mainly Salix herbacea *leaves and shoots; 2: Barley straw (small mesh bags); 3: Barley straw; 4: Mixed site litter, mainly* Salix *(on surface).*

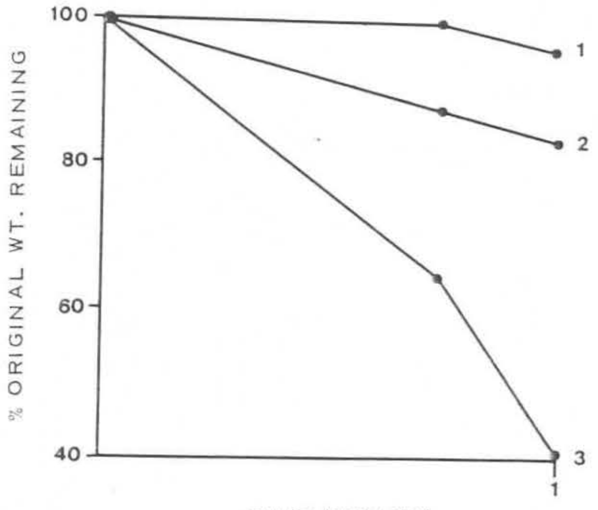
Fig. 1 (Cont'd).



Hardangervidda, Birch Forest, September 1969-72. 1: Mixed site litter (on surface); 2: Mixed ite litter (small mesh bags); 3, 4: Mixed site litter; 5, 6: Barley straw; 7: Barley straw (small iesh bags). .... = Ao/A_2 horizon.



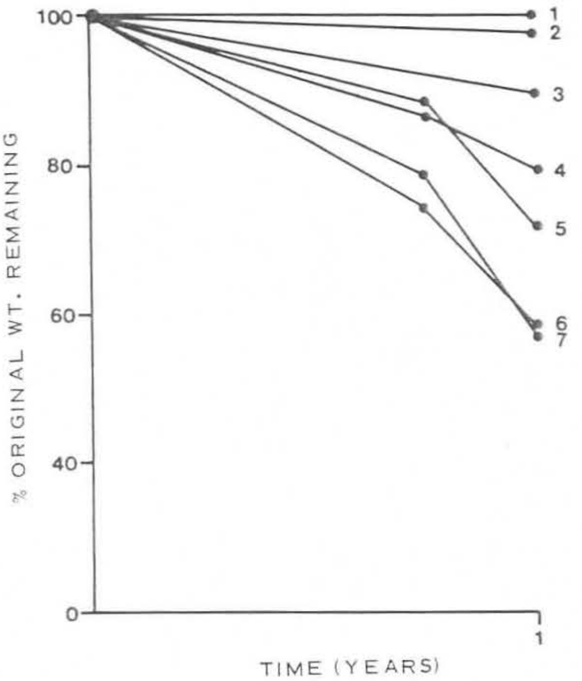
j. Hardangervidda, Lichen Heath, September 1971-72. 1: Juncus trifidus *leaves (on surface); 2:* Festuca ovina *leaves (on surface); 3: Lichens; 4:* Carex bigelowii *leaves; 5:* Vaccinium *sp. leaves (on surface).*



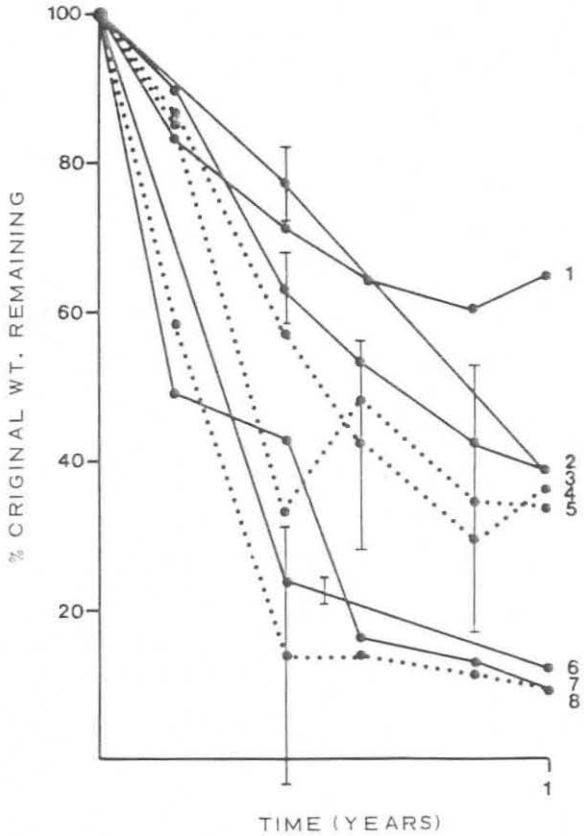
k. Hardangervidda, Dry Meadow, September 1971-72. 1: Dryas octopetala; *2: Mixed mosses; 3: Mixed site litter, except* Dryas.

Fig. 1 (Cont'd).

different curves, each representing a different chemical constituent of the litter. The curves in Fig. 1 were tested by regression against several types of curves, including exponential. They generally conform fairly well to a negative exponential pattern except in the initial period, when there is a higher loss from most litters than can be accounted for by a simple negative exponential curve, probably due to leaching. However, some show considerable variation about that pattern, e.g. *Stilbocarpa* lamina at Macquarie Island (Fig. 1 m), and



l. Hardangervidda, Wet Meadow, September 1971-72. 1: Drepanocladus uncinatus; *2:* Philonotis fontana; *3: Other mosses; 4:* Carex nigra *roots (inserted vertically in the soil); 5:* Salix *spp. leaves and shoots; 6:* Carex nigra *leaves; 7: Roots other than* Carex *(inserted vertically).*

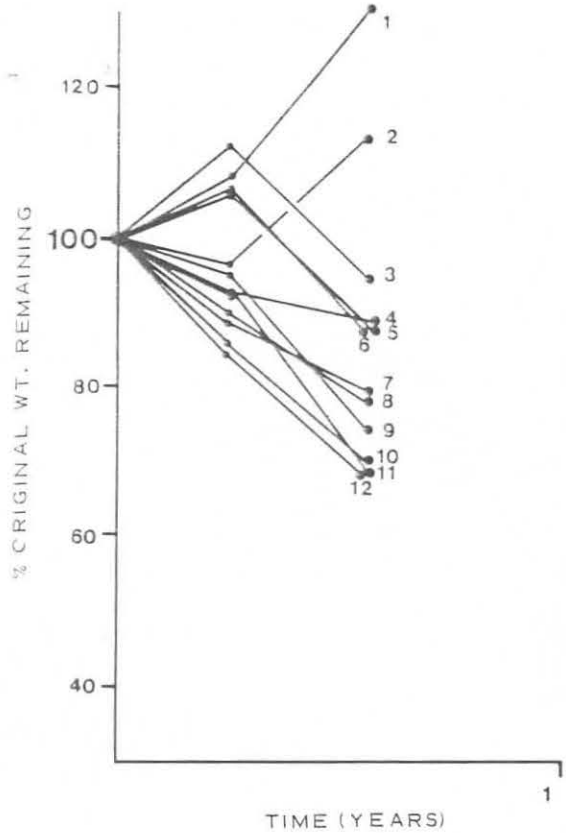


m. Macquarie Island, December 1969-70. 1, 5: Pleurophyllum hookeri *lamina; 2:* Poa foliosa *sheath; 3, 4:* Poa *lamina; 6:* Stilbocarpa polaris *petiole; 7, 8:* Stilbocarpa *lamina.* ——— *Fenced site,* ..... *Unfenced site.*

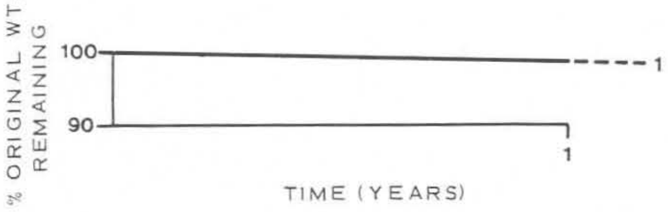
Fig. 1 (Cont'd).

Eriophorum and *Juncus* leaves at Moor House (Fig. 1 a), while others show accelerated losses in the later stages of decay. While the present data are too sparse to be conclusive, they suggest that a negative exponential is not an adequate description of the relationships between litter quality and loss rates over time.

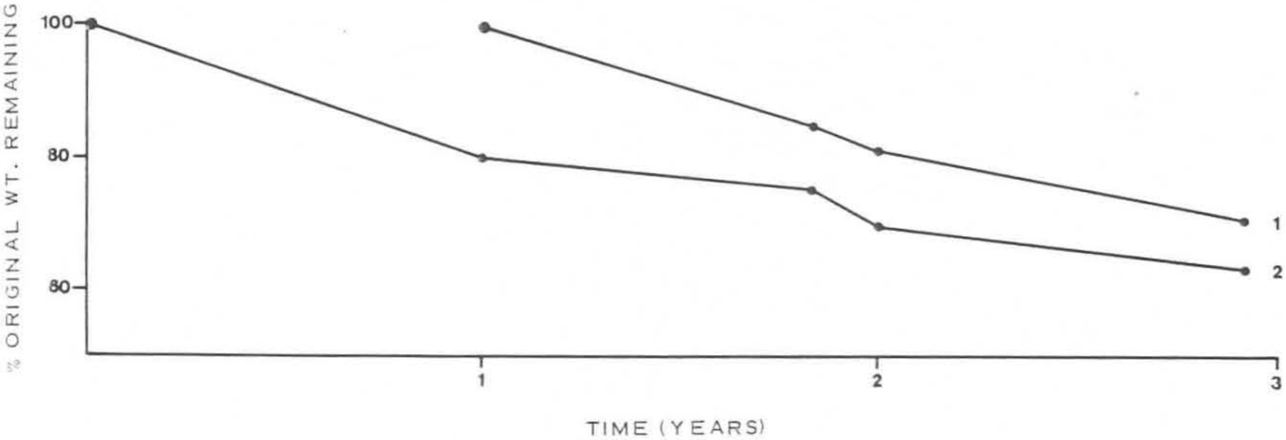
4. There is little indication of any broad seasonal patterns. In some cases there is no discernible pattern, e.g. Macquarie Island (Fig. 1 m), Glenamoy (Fig. 1 n), probably related, in the case of Macquarie Island, to the relatively uniform climatic conditions (French, this volume). In sites with more marked climatic variation any major differences between summer and winter losses are obscured by a high initial loss which occurs independently of the time of year. Kärenlampi (1971) has carried out intensive sampling during summer (Fig. 1 q) at Kevo. His results indicate that short-term variations in climate, particularly in cumulative factors, such as drought, are more important than general seasonal trends. Seasonal patterns of weight loss may also be obscured by the insensitivity of the method when the losses measured are small.



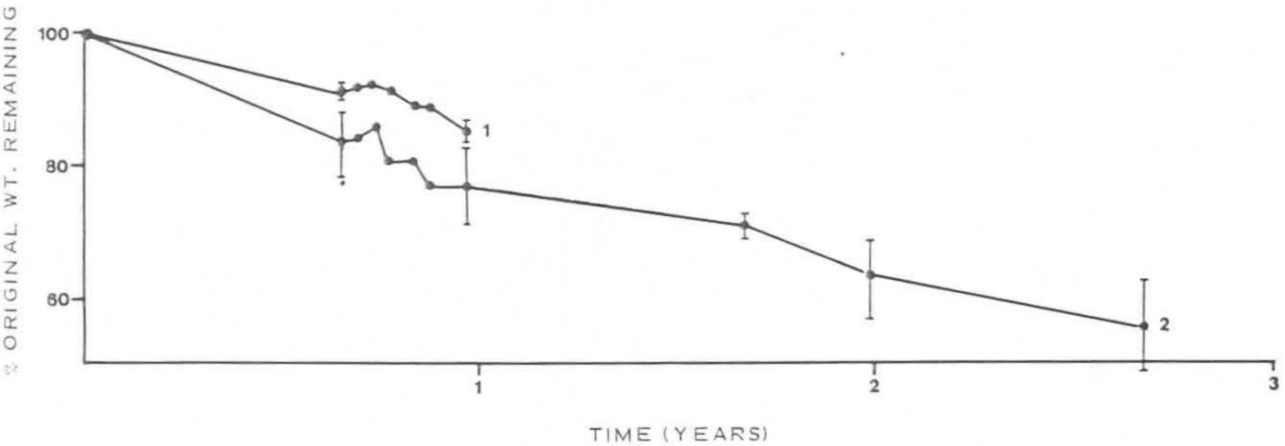
n. Glenamoy Bog, March 1971. 1: Calluna *shoots (GD); 2:* Myrica gale *leaves (GD); 4:* Eriophorum vaginatum *leaves (DD); 5:* Molinia *leaves (DD); 9:* Trichophorum *leaves (GW); 10:* Molinia *leaves (GD); 11:* Schoenus *leaves (GW); 12:* Myrica *leaves (GW); GW = Green, wet; GD = Green, dry; DD = Dead, dry.*



o. Signy Island. 1: Chorisodontium aciphyllum.

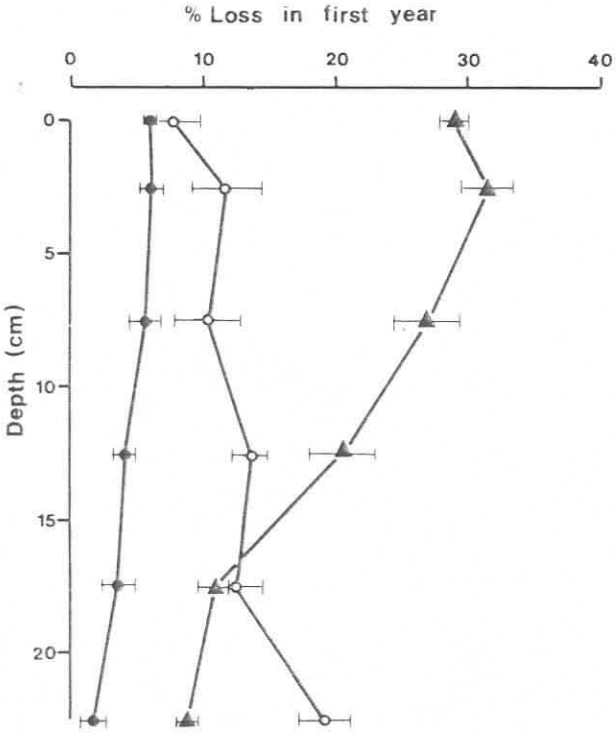


p. Devon Island, Mesic Meadow, August 1970-73. 1, 2: Carex stans *leaves.*

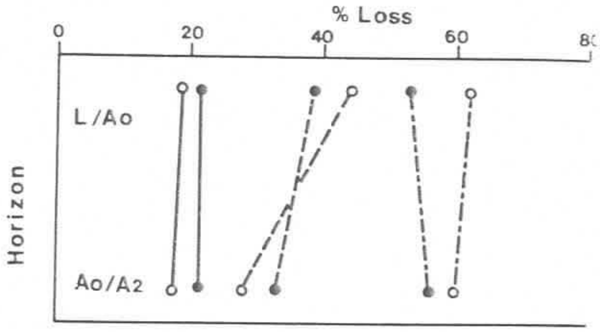


q. Kevo, October 1969-72. 1: Pinus sylvestris *needles in Pine site; 2:* Betula tortuosa *leaves in Birch site.*

Fig. 1 (Cont'd).



a. Moor House, Bog, October 1970-71. ● Calluna *stems;* ○ Eriophorum vaginatum *roots;* ▲ Juncus effusus *leaves.*



b. Hardangervidda, Birch Forest, 1970-71. ● *Mixed site litter;* ○ *Barley straw;* —— *after 3 months;* – – – – – *after 15 months;* – · – · – *after 27 months.*

Fig. 2. Variation in percentage dry weight losses with depth.

5. Limited data from Hardangervidda and Moor House (Fig. 2) show that the loss rate of the same litter can vary in different parts of the soil profile.
6. Statistical errors, where available, vary widely. In most cases, standard errors are less than ± 30% of the mean, but in others they are up to ± 100% of the mean or more. Most of the Glenamoy results have large errors. The variation in the size of errors results from differences in sampling intensity, the number of replicates varying between 3 and 30, as well as from microhabitat and methodological variation.

Variation in weight loss can thus be attributed to variation in:

a. Litter "quality", e.g. chemical composition, physical structure.
b. Site factors: climate and soil conditions.
c. Position in the soil profile.
d. Time in the field, i.e. change in quality and environment with age.

To these can be added:

e. Structure of decomposer population: abundance and physiological groups.
f. Methodology.

Since tundra sites do not appear to lack any major physiological groups of microorganisms (Dunican & Rosswall, and Flanagan & Scarborough, this volume) and large litter-feeding fauna, such as earthworms, are generally absent, the effect of the decomposer organisms is more likely to be from variation in their activity, caused by the other factors listed, than from variation in population structure. Methodological variation is also unlikely to seriously bias the results at the level of resolution sought here.

Analyses of First Year Losses of Litter in or on the Litter Layer

To examine in more detail the variation in weight loss between sites, variation with depth and time are eliminated by selecting only data from a standard depth and time period. The losses in the first year from litter in or on the litter layer will therefore be examined here. Profile data and time-series will be examined later, to see how the initial loss pattern is modified by the effects of depth and time.

Preliminary examination of data

Table 1 contains the mean percent weight loss in the first year of all litters in sites for which site data were available. Some additional results, where details of site conditions were not available, are given in Table 3. Without reference to the observed weight losses, the litters have been grouped into six categories: Mosses, Lichens, Wood, Shrub shoots, "Hard" Leaves and "Soft" Leaves. The criteria for the first four of these are taxonomic and morphological. The other two categories are distinguished on the basis of chemical composition, particularly proportions of lignins, polyphenols, soluble carbohydrates and inorganic nutrients, plus physical hardness. Where sufficient information on these was not available, a subjective assessment of chemical quality was made, based on taxonomic affinities.

The sites also have been partitioned by 1) temperature patterns (Warm Oceanic, Warm Continental, Cold Oceanic, Cold Continental), 2) moisture (wet, mesic, dry), 3) pH (greater or less than 4.5), on the basis of the site classifications (French, this volume), and 4) vegetation (modified from Wielgolaski, 1973). The site and litter categories are listed in Table 1.

The basic set of 91 data from 62 litters in 23 sites (Table 1) show that most of the first year losses are in the range 0-40% (Fig. 3). Higher losses are recorded almost exclusively at Macquarie Island and Glenamoy.

From the various site and litter categories, cumulative percentage frequency curves of first year loss rates in each category have been plotted (Fig. 4a-g). The following trends are apparent:

1. Mosses, Lichens and Wood have lower loss rates than Hard Leaves and Shrub shoots, which in turn have lower rates than Soft Leaves (Fig. 4a). Much of the difference between Hard and Soft Leaves, however, is the effect of the Macquarie Island data.

2. Warm Oceanic sites appear to have a higher proportion of high losses than do all the other three temperature groups, though the results for the Warm Continental

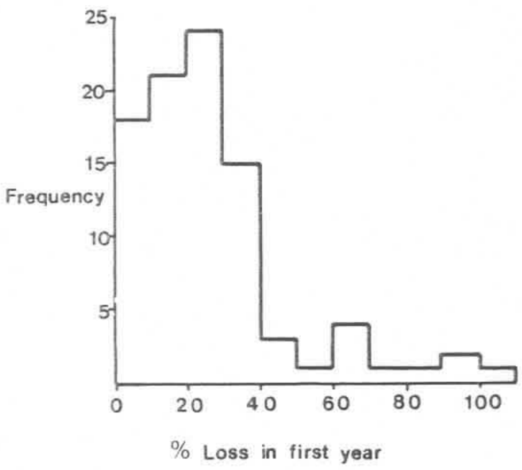


Fig. 3. Frequency distribution of percentage dry weight losses in the first year from litters at tundra sites, compiled from the data in Table. 1.

Table 1. Basic comparative data set of percentage loss in 1st year of litter for tundra sites for which soil and climatic data were available. Site and litter type categories included.

All litters are in bags with medium (about 1 mm) mesh size, except at Macquarie I. and Moor House, where nets (about 1 cm) were used, unless otherwise stated. All litters are on the litter surface, except some of the Norwegian litters, which are placed in the litter layer. Where more than one result is available for any litter (e.g. from different years or microhabitats) they are given separately.

Site and litter legend:

Litter: M Moss; L Lichen; W Wood; S Shrub Shoots; HL "Hard" Leaves; SL "Soft" Leaves

Temperature: WO Warm Oceanic; WC Warm Continental; CO Cold Oceanic; CC Cold Continental

Moisture: W Wet; M Mesic; D Dry

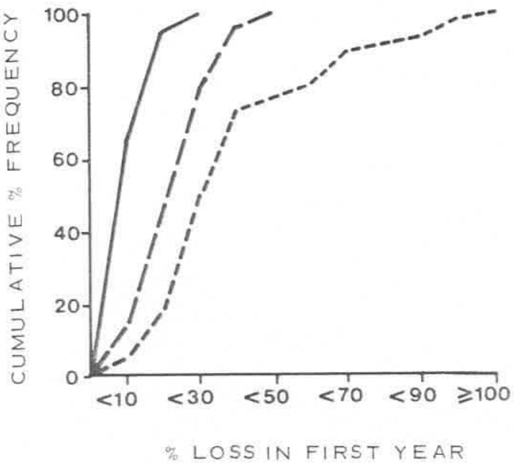
pH: + above 4.5; – below 4.5

Vegetation: MP Moss Peats; H Heath; S Snowbed; SB Shrub Bog; F Forest; MB Monocot Bog; TM Tundra Meadow

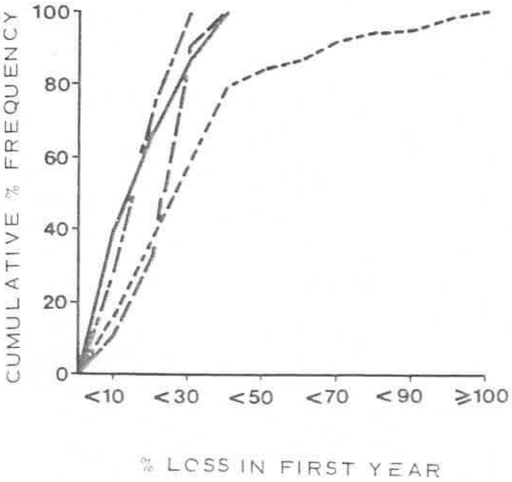
Site	Subsite	Litter	Percentage loss in first year	Litter and site categories: Litter	Temp	Moisture	Soil pH	Vegetation	Source of data
Macquarie I., Australia	M1	*Poa foliosa* lamina	61 64	SL	WO	M	+	TM	J.F. Jenkin (personal communicat
		Poa foliosa sheath	62	SL					
		Stilbocarpa polaris lamina	90 91	SL					
		Stilbocarpa polaris petiole	88	SL					
		Pleurophyllum hookeri lamina	36 66	SL					
Signy I., Antarctica	*Chorisodontium*	*Chorisodontium aciphyllum*	1	M	CO	W	–	MP	J.H. Baker (1972 and personal communication)
	Drepanocladus	*Drepanocladus uncinatus*	14 24	M	CO	M-W	+	MP	N.J. Collins (personal communicat
S. Georgia	*Festuca* grassland								
	(70 m)	*Festuca erecta* leaves	25	SL	CO	M	+	TM	Smith & Stephenson (in press)
		Poa flabellata leaves	12	SL					
	(230 m)	*Festuca erecta* leaves	20	SL	CO	M	+	TM	
		Poa flabellata leaves	30	SL					
	(350 m)	*Festuca erecta* leaves	22	SL	CO	M	+	TM	
		Poa flabellata leaves	22	SL					
Devon I., Canada	Mesic meadow	*Carex stans* leaves	21 19	SL	CC	W	+	MB	P. Widden et al. (1972 and personal communication)
Kevo, Finland	Pine site	*Pinus sylvestris* needles	15	HL	WC	D	–	F	L. Kärenlampi (1971 and MAD*)
	Birch site	*Betula tortuosa* leaves	24	SL	WC	D	–	F	
Glenamoy, Ireland	Bog	*Trichophorum caespitosum* leaves	22	HL	WO	W	–	MB	P. Dowding (MAD*, personal communication and 1972)
		Schoenus nigricans leaves	10	HL					
		Molinia caerulea leaves	30	SL					
		Eriophorum vaginatum leaves	20	SL					
	Grassland	*Festuca arundinacea* leaves	100	SL	WO	W	+	MB	
	Forest	*Molinia caerulea* leaves	70	SL	WO	W	+	F	
Hardangervidda, Norway	Lichen heath	Barley straw	10	HL	WO	D	–	H	A.K. Veum (MAD* and personal communication)
		Mixed site litter, vascular plants	12	HL					
		Mixed lichens	5 16	L					
		[illegible]	[illegible]	[illegible]					

		Mixed site litter, vasc. other than *Dryas*	38	59	SL					
		Mixed site mosses	17		M					
	Wet meadow	Barley straw	20		HL	WO	W	+	MB	
		Mixed site litter, vascular plants	33		SL					
		Mixed site mosses	4		M					
		Carex nigra leaves	41		SL					
		Salix sp. shoots	28		S					
		Philonotis fontana	2		M					
		Drepanocladus uncinatus	0		M					
		Other mosses	11		M					
	Birch forest	Barley straw	38		HL	WO	M	–	F	
		Barley straw (small mesh bags)	40		HL					
		Mixed site litter	36	33	HL					
		Mixed site litter (small mesh bags)	32		HL					
	Snow bed	Barley straw	23		HL	WO	D	–	S	
		Barley straw (small mesh bags)	18		HL					
		Mixed site litter, mainly *Salix herbacea*	18	38	S					
Abisko, Sweden	Stordalen mire	*Rubus chamaemorus* leaves (bags)	16	24	SL	WC	D	–	SB	T. Rosswall (1973 and personal communication)
		Rubus chamaemorus leaves (strings)	32		SL					
		Empetrum hermaphroditum leaves and stems	6		S					
		Betula nana leaves	21	30	SL					
		Betula nana twigs (strings)	8		S					
		Andromeda polifolia leaves and stems	15		S					
		Sphagnum fuscum	0		M					M. Sonesson (1973)
		Sphagnum balticum	6		M					
		Sphagnum riparium	10	5	M					
		Sphagnum lindbergii	7		M					
		Sphagnum recurvum	5		M					
Moor House, UK	Bog	*Calluna vulgaris* stems (strings)	8	7	W	WO	W	–	SB	O.W. Heal & P.M. Latter (personal communication)
		Calluna vulgaris shoots (bags)	15	20	S					
		Eriophorum vaginatum leaves	22	26	SL					
		Eriophorum angustifolium leaves	24		SL					
		Eriophorum angustifolium leaves (bags)	18		SL					
		Rubus chamaemorus leaves	36	38	SL					
		Juncus effusus leaves	31		SL					
		Narthecium ossifragum leaves	45		SL					
		Nardus stricta leaves	23		HL					
		Trichophorum caespitosum leaves	18		HL					
		Pinus contorta needles	25		HL					
		Sphagnum spp.	17		M					R.S. Clymo (1965)
	Juncus	*Juncus squarrosus* leaves (bags)	21		SL	WO	W	–	MB	P.M. Latter & J.B. Cragg (1967)
Barrow, USA	Site 2	Mixed site litter	6		SL	CC	W	+	MB	P.W. Flanagan (personal communication)
		Dupontia fischeri leaves	16		SL					R. Benoit, Campbell & Harris (1972)

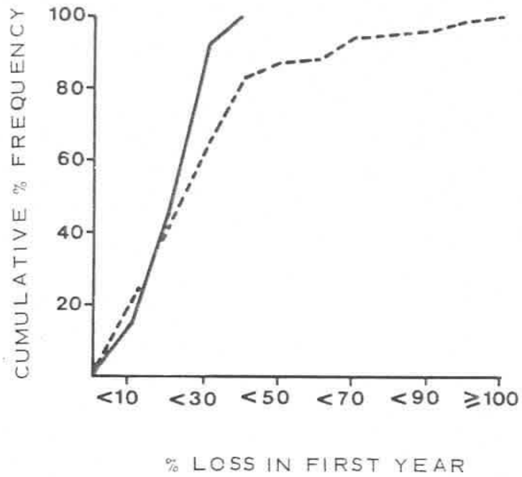
* Microbiology and Decomposition Data Bank.



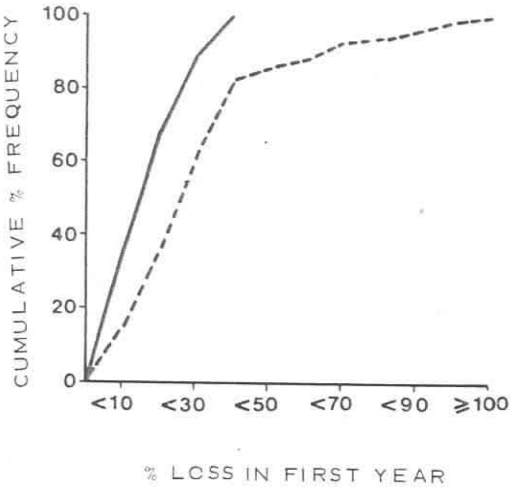
a. Litter type; ——— *Mosses, lichens and wood;* — — — *Hard leaves and Shrub shoots;* ---- *Soft leaves.*



b. Temperature pattern: ---- *Warm Oceanic;* ——— *Warm Continental;* — — — *Cold Oceanic;* -·-·- *Cold Continental.*



c. Temperature pattern: ---- *Warm;* ——— *Cold.*



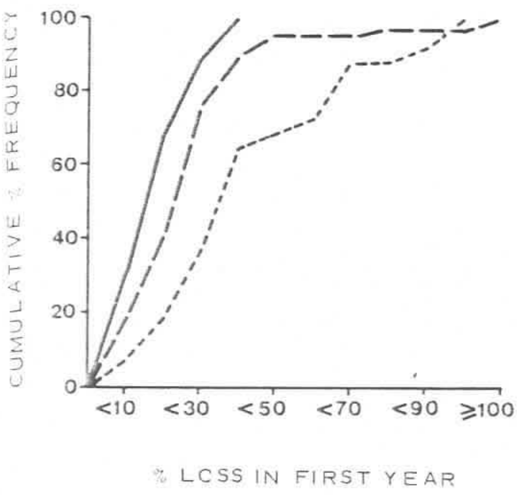
d. Temperature pattern: ---- *Oceanic;* ——— *Continental.*

Fig. 4. Cumulative percentage frequency curves for first year % losses from all litters, divided according to the litter and site categories listed in Table 1.

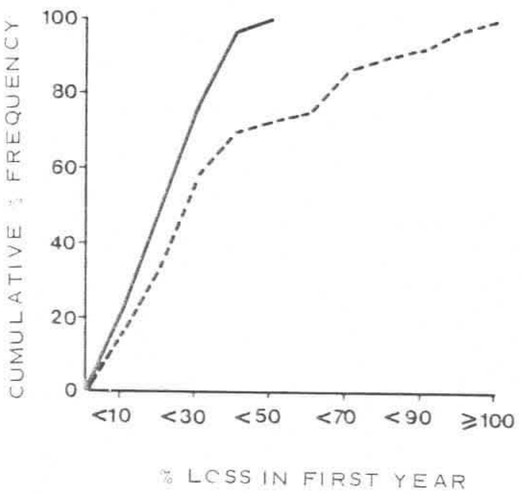
group are biased by a low proportion of Soft Leaves (Fig. 4b). Comparing Warm and Cold sites (Fig. 4c) and Oceanic and Continental sites (Fig. 4d), oceanicity appears to have at least as much effect as actual temperature, indicating interaction of temperature and moisture effects.

3. The importance of moisture is further indicated in Fig. 4e, with a clear increase in losses from dry to wet to mesic sites. The one exception is the high loss from *Festuca* leaves on the wet Glenamoy Grassland.

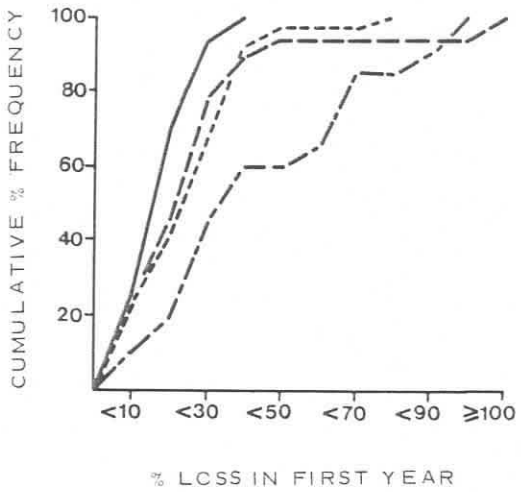
4. pH also appears to have some effect (Fig. 4f), with "acid" sites (pH < 4.5) having lower losses than "alkaline" ones (pH > 4.5).



e. Moisture: — — — Wet; ---- Mesic; ——— dry.



f. pH: ——— below 4.5; ---- above 4.5.



g. Vegetation: ——— Moss peats, heaths and Snowbeds; — — — Monocot bogs and mires; ---- Shrub bogs and forests; -·-·- Tundra meadows.

Fig. 4 (Cont'd).

5. Some of the interdependence of the various site and litter categories is shown in Fig. 4g, where losses increase from moss peats, heaths and snow beds, through various bog and forest types, to tundra meadows. The first of these three groups tend to be cold or dry sites with a high proportion of cryptogams and woody plants, the bog sites are all the wettest sites, and the meadows are all oceanic, mesic, and usually warm sites, with a high proportion of Soft Leaves. There is a marked similarity between the curves for the vegetation types (Fig. 4g) and for moisture categories (Fig. 4e), emphasising the importance of moisture, but indicating that its action can be indirect, through its effects on vegetation composition, as well as direct by affecting microbial and faunal activity.

Since some of the differences between site groups may thus result from differences in litter quality rather than site differences, (1, 2, 5 above), the curves for temperature, moisture and pH groups were recompiled using only the data for Soft Leaves. This eliminates some of the variation resulting from litter quality. The resulting curves

repeat the patterns shown for all litters. Differences between temperature groups are accentuated as also are those between pH groups. The moisture curves remain about the same as those for all litters.

Tests for statistically significant differences between losses in the various site and litter categories

A Kolmogorov-Smirnov two-sample test (Siegel, 1959) was used to test the statistical significance of the differences observed in the cumulative frequency curves. Since sample (i.e. group) sizes were extremely variable, a chi-squared approximation was used throughout, though this gives a conservative test for small samples, particularly if there is a large discrepancy in sample sizes.

As expected from the visual comparison of the curves, discussed above, litter quality and moisture are the most significant factors (Table 2). Most of the site groupings, however, are arbitrary divisions of a continuous gradient, and the results should be interpreted in the light of this. For example the moisture partitions indicate a curvilinear relationship with moisture.

Table 2. Results of Kolmogorov-Smirnov tests.

Partition tested	All litters				Soft leaves only			
	D	n_1	n_2	χ^2	D	n_1	n_2	χ^2
(a) Litter Quality								
Moss/lichen/wood<hard leaves/shrub	.49	19	28	10.87**				
Hard leaves/shrubs<soft leaves	.29	28	44	5.76				
(b) Temperature								
Warm oceanic>all others	.30	63	28	6.98*	.49	28	16	9.78**
Warm oceanic>warm continental	.30	63	15†	4.36	.43	28	6†	3.65
Warm oceanic>cold oceanic	.30	63	9†	2.84	.51Δ	28	6†	5.14
Warm oceanic>cold continental	.41Δ	63	4†	2.53	.68	28	4†	6.47*
Warm continental<cold oceanic	.34	15	9†	2.60	.16	6	6†	0.31
Cold continental<cold oceanic	.42Δ	4	9†	1.95	.63Δ	4	6†	3.81
Warm>cold	.28	78	13	3.49	.52	34	10	8.36*
Oceanic>continental	.32	72	19	6.16*	.39	34	10	4.70
(c) pH								
"Acid" (<4.5)<"Alkaline" (>4.5)	.28	55	36	6.82*	.42	20	24	7.70*
(d) Moisture								
Mesic>wet	.38	26	37	8.82*	.39Δ	16	19	5.28
Wet>dry	.27	37	28	4.65	.25	16	9	1.53
Mesic>dry	.51	26	28	14.03***	.50Δ	16	9	5.76
Mesic>all others	.44	26	65	14.38***	.43	16	28	7.53*
All others>dry	.36	63	28	10.05**	.35	35	9	3.51
(e) Vegetation								
Meadows>moss peats/heaths/snowbeds	.49	20	16	8.54*				
Meadows>shrub bogs/forests	.37	20	37	7.11*				
Meadows>monocot bogs	.34	20	18	4.38				
Shrub bogs>moss peats/heaths/snowbeds	.26	37	16	3.02				

† These partitions may give excessively conservative tests, because of the large imbalance in sample size, especially with small n_2. Partitions where D may indicate a real difference, though χ^2 is not significant, are marked Δ.

*,**,*** χ^2 significant at 5%, 1% and 0.1% levels.

The interrelationships of site and litter factors seen in the frequency curves are reflected in the differences between the results for all litters and for Soft Leaves. The differences result, at least in part, from the relative proportions of the various litter types used at each site, since most workers have used representative site litters. Thus dry sites, for example, have lower losses than wet or mesic sites, but also tend to have a greater proportion of resistant litters.

Some of the statistical results for the temperature partitions are excessively conservative, owing to the large differences in sample size. Those which are considered to be real differences, though chi-squared is not significant, are indicated in Table 2.

Although causal relationships cannot be determined from the analysis, the results indicate that:

1. Litter quality, temperature, moisture, soil pH and vegetation composition all influence litter decay rates.
2. Litter quality and moisture are the most important single factors among those tested.
3. The effects of temperature, moisture, vegetation, litter quality and, perhaps, pH, are all interrelated.

Relation between loss rates and site characteristics

The Kolmogorov-Smirnov tests show that, despite the large variation related to litter quality, there are significant differences in loss rates between sites. Together with the cumulative frequency curves, the tests also indicate that the effects of many of the site factors are themselves closely interrelated.

To examine the effects of a number of variables in combination, and to allow for intercorrelation of variables, litter losses were examined in relation to the principal component analyses (P.C.A.) used in the site classification (French, this volume).

The P.C.A.s define a series of more or less complex environmental gradients (vectors or components) on the basis of the intercorrelations of a variety of soil and climatic variables. Because these components are defined statistically, they are not always directly interpretable biologically, pedologically or climatologically. However, in these analyses most of the components were readily interpretable, particularly in one analysis which included soil nutrient and soil temperature data (Analysis I b). This analysis was therefore chosen for the comparison of loss rates with site factors.

Loss rates were examined in relation to all significant components of Analysis I b. Fig. 5 and 6 show the positions of the decomposition sites along components I and IV (component values), with loss rates for each site superimposed. Component I is a gradient from warm, wet, organic, high-N to cold, dry, mineral, low-N conditions. Component IV is a trend from acid sites with low phosphorus, calcium and C/N ratio to alkaline sites with high P, Ca, C/N. These two components gave the best relationships with litter losses, and represent climatic and soil quality gradients. Fig. 5 shows maximum and minimum loss rates for all litters, while Fig. 6 shows mean losses from Soft Leaves. Both suggest a trend of increasing losses from cold, dry, acid, mineral sites with low P, Ca and N to warm, wet, alkaline, organic sites with high P, Ca and N. The Soft Leaf decay rates (Fig. 6) accentuate the pattern shown in Fig. 5 because of the reduction in variation due to litter quality. Conversely Hard Leaves, Shrub shoots, Mosses, Lichens and Wood did not show any trend related to the components of analysis I b, probably because their losses are limited more by their own composition than by site conditions.

Macquarie Island, S. Georgia, and the Signy Island *Drepanocladus* sites were not included in the P.C.A., because certain soil data were not available in time. Their approximate positions, estimated from the data available, are indicated in Fig. 5.

To examine further the relation between loss rates and site component values, single and multiple regressions were calculated, using linear quadratic and exponential expressions of the site component values, both additively and multiplicatively.

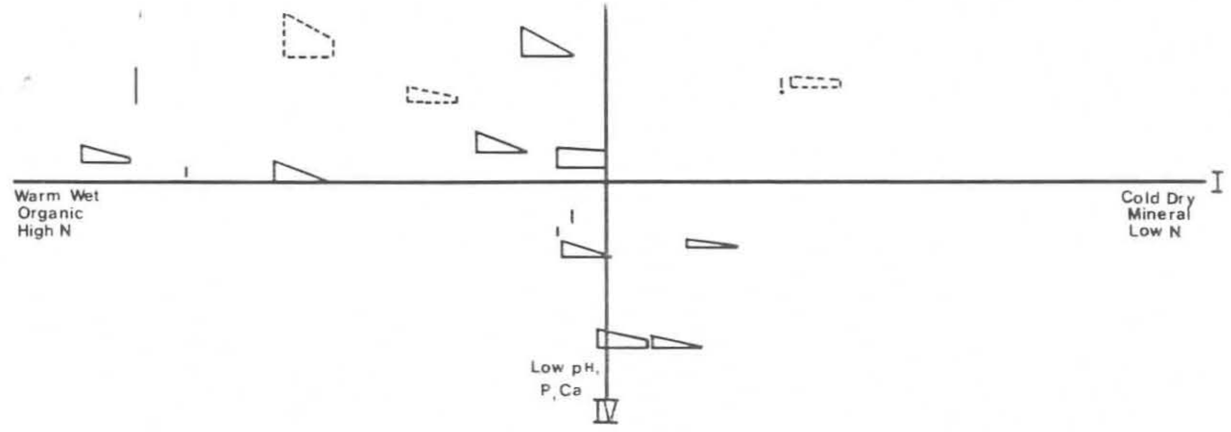


Fig. 5. Maximum and minimum first-year % losses of litters at tundra sites in relation to the position of the sites along Components I and IV of Site Classification I(b) (French, this volume), based on climatic and soil data, including soil nutrients. The heights of the left and right sides of the quadrangles are proportional to maximum and minimum % losses. Estimated positions of three sites not included in this classification, and % losses at those sites are shown by the broken quadrangles. Left to right — Macquarie Island, S. Georgia, and Signy Island Drepanocladus. *Where only one result was available, this is given as a single vertical line.*

Four sets of regressions were run, using all litters, Soft Leaves, maximum rates for each site and maximum rates for Soft Leaves, thus progressively reducing variation due to litter quality. Signy Island *Chorisodontium* and Moor House *Juncus squarrosus* were excluded from the last two sets, as the losses from these two species were not considered to be representative maxima for those site conditions.

The exponential regressions all gave low correlation, generally less than the linear regressions. This result contrasts with that for bacterial numbers, which showed good exponential relationships with the components of analysis Ib (Holding, Collins, French, D'Sylva & Baker, this volume), indicating that microbial population estimates are not necessarily good indices of activity, or that bacteria are not major agents of decomposition.

The other regressions (linear and quadratic) all gave improved correlations as litter quality effects were progressively removed. The regression coefficients are very similar in comparable regressions from "all litters" through to "maximum rates for Soft Leaves," indicating that the improved correlations result from the removal of variation related to litter quality.

Components I and IV gave the best single correlations throughout, but even when maximum rates were used in the regressions no single component accounted for more than 50% of the variation.

In the multiple regressions, components I and IV again gave the most consistently good correlations. Component I (climate) became progressively more important relative to Component IV (soil) as litter quality variation was removed. Except in the case of maximum rates and maximum rates for Soft Leaves, Component IV gave the only significant quadratic term, but in these two sets there was also a significant quadratic effect of Component I.

Regression surfaces were produced for maximum rates, and maximum Soft Leaf rates, with Components I and IV, including quadratic terms, additively and multiplicatively. The component values for the multiplicative regressions were first adjusted to avoid zero values, by subtracting 5 from all values of Component I and adding 5 to all values of Component IV. The regression surfaces, for maximum rates, together with the regression equations and plots of observed values against those

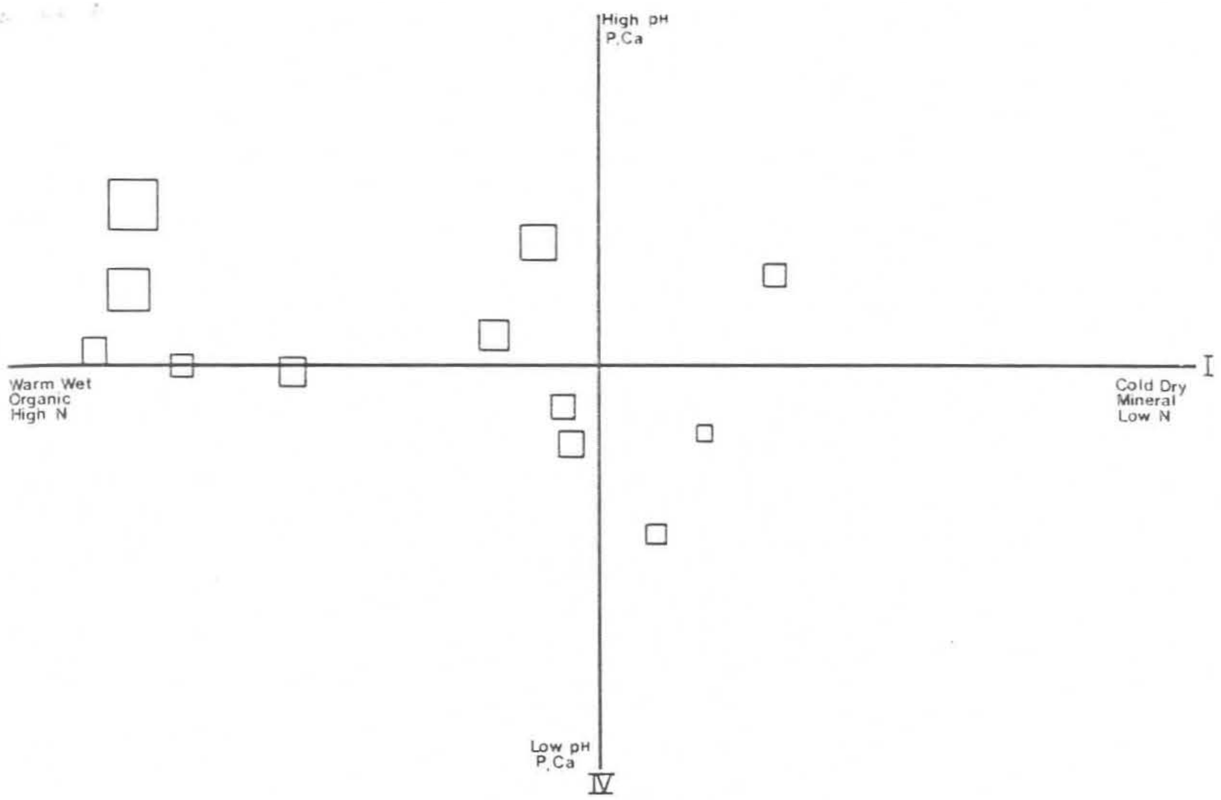


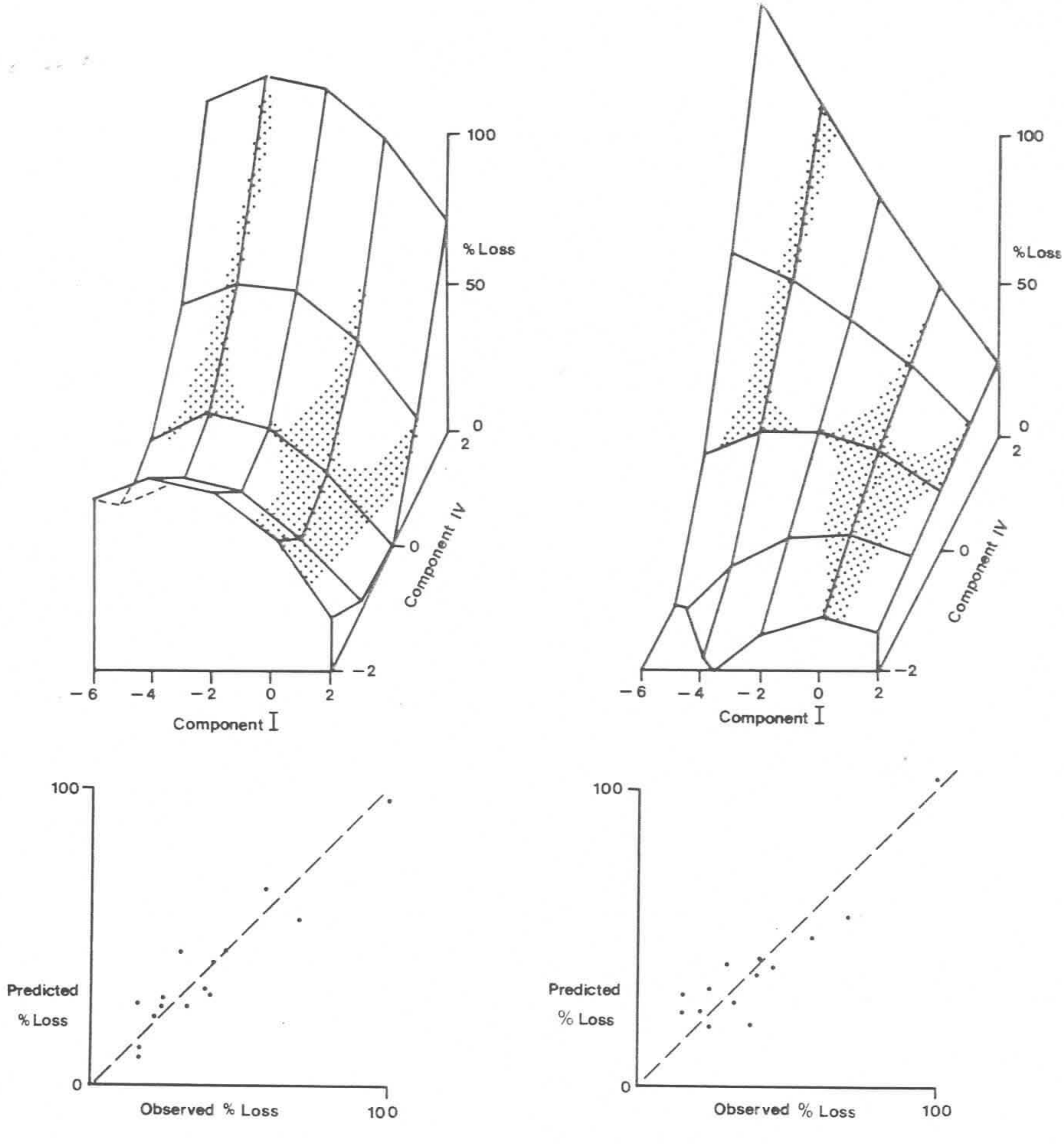
Fig. 6. Mean first-year % losses of soft leaves at tundra sites in relation to the positions of the sites along components I and IV of Site Classification I(b) (French, this volume), based on climatic and soil data, including soil nutrients. The areas of the squares are proportional to the first-year % losses.

predicted by the regessions are given in Fig. 7. The surfaces for maximum Soft Leaf rates are very similar but give lower rates in the dry sites (e.g. Hardangervidda Lichen Heath). In these sites the highest losses are from shrub leaves rather than Soft Leaves, possibly related to greater water retention in the former.

The correlations for additive and multiplicative regressions are very similar although the regression surfaces (Fig. 7) are obviously very different. This is because most of the data lie in a band across the two components (shaded area in Fig. 7) and in this region the regression surfaces have similar shapes. Although there is little to choose between the regressions statistically, it seems likely that each component will become absolutely limiting at some point, irrespective of the value of the other. For example if a site is extremely dry it does not matter how high soil nutrient levels are, decay rates will still be very low. This, combined with examination of the shapes of the surfaces, indicates that the multiplicative surfaces probably provide the best description of the relationship.

These results suggest that:

1. Litter quality is the most important factor limiting decay rates, followed by soil conditions, particularly availability of phosphorus and calcium, then by climate.
2. The effects of soil and climatic conditions are interactive.
3. The two main effects of site factors are: increasing losses with increasing soil nutrients, following a quadratic or similar curvilinear pattern, and a curvilinear "hump" effect with temperature and moisture. Respiration studies (Flanagan & Veum, this volume) give experimental corroboration of the latter effect.



a. Percent loss $= 26.34 - 10.94 \times CI - 1.49 \times CI^2 + 13.5 \times CIV + 11.5 \times CIV^2$ ($R = 0.93$).

b. Percent loss $= -12.575 - 5.95 \times CI \times CIV + 0.63 \times CI \times CIV^2 - 0.755 \times CI^2 \times CIV + 0.114 \times CI^2 \times CIV^2$ ($R = 0.914$).

Fig. 7. Additive (a) and multiplicative (b) regression surfaces for maximum first-year % losses in relation to Components I and IV of Site Classification I(b) (French, this volume). Plots of observed values against those predicted by the regressions are given below each regression surface. The shaded areas show the part of the surfaces covered by the data used in the regressions.

Relation between loss rates and specific soil and climatic variables

In an attempt to express the general trends observed in the comparisons with site component values in terms of actual site variables, a number of regressions were calculated on specific site variables which seemed, from the P.C.A. and other analyses, to be important in decomposition.

Temperature-moisture interactions were obviously important (Component I and Kolmogorov-Smirnov tests). The sum of degree days for days with mean temperature above 0°C in the surface soil horizon was used to express site temperatures, while moisture was expressed as mean soil moisture in grams per gram dry weight of soil.

Many soil variables, such as pH and nitrogen, were shown by the P.C.A. to be highly correlated with temperature and moisture variables, so these were not used. Calcium and phosphorus were shown to be important variables (in Component IV), and are not well correlated with any climatic variables, so "available" phosphorus and calcium were used to represent soil "quality."

Only maximum loss rates were regressed, to minimise the effects of litter quality. S. Georgia data and a mean maximum rate for the Signy Island sites were included.

First, weight losses were regressed against temperature sum and moisture, multiplicatively, with quadratic and cubic moisture terms. This produced the temperature-moisture "hump" (Fig. 8), which accounted for 59% of the total varia-

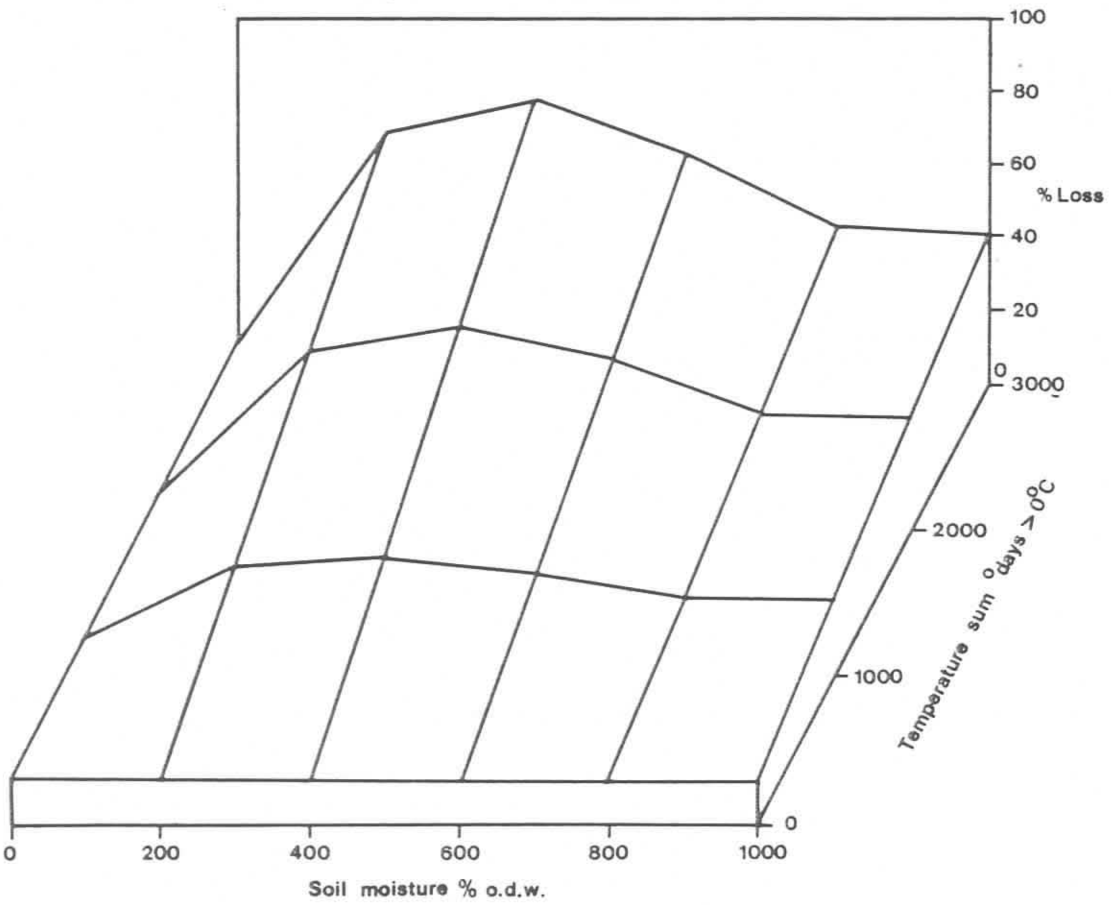


Fig. 8. Regression surface for maximum first-year % losses of litters in tundra sites, in relation to temperature sum and soil moisture. Percent loss = $11.62 + 0.0147 \times T \times W - 0.00289 \times T \times W^2 + 0.000152 \times T \times W^3$ ($R = 0.769$), where T = sum of degree-days for days with mean soil temperature (5 cm) above 0°C, W = ½ (max + min) soil moisture (g/g.d.w.).

tion. This regression surface appears fairly reasonable except at 0°days and absolute dryness, where, instead of the expected very low or zero values, a loss of 11.6% is predicted.

Additional problems occur with the addition of calcium and phosphorus to the regression. Are their effects linear or curvilinear? If the latter, in which direction? They will each interact with the temperature-moisture "hump," but do they do so independently, or do they also interact with each other? There is very little information available on these points. However, some analyses by Heal (in press) and Van Cleve (this volume) of the effects of nutrients in litter on loss rates suggest an approximately logarithmic or asymptotic relationship with both calcium and phosphorus. A preliminary series of regressions, using linear and logarithmic expressions of calcium and phosporus, indicated a similar pattern for both nutrients in soil, so a further series was calculated, combining logarithmic transformations of calcium, or phosphorus, or both, with the temperature-moisture hump. R^2 values ranged from 0.77 for the totally interactive regression ($\log_e P \times \log_e Ca \times T \times (W + W^2 + W^3)$) to about 0.9 for various regressions containing independent expressions of phosphorus and calcium, but there are no major differences between the regression surfaces produced by the various regressions, except on considerable extrapolation. All the regressions including soil nutrients accentuate the "hump" effect as nutrient levels increase, i.e. loss rates remain low at low temperature and moisture levels, irrespective of nutrient levels, but as nutrient levels increase, rates under optimal climatic conditions increase. At present, there is no evidence on which to decide between any of the regressions.

The above regressions confirm the conclusions drawn from the relationships of loss rates to site component values:

1. Provided litter quality is not severely limiting, loss rates are related to soil nutrient status, temperature and moisture.
2. Temperature and moisture effects are interactive, and can be represented by a "hump," wherein decay rates increase with the temperature sum at a site, and increase with soil moisture up to about 400% of dry weight. Above 400%, losses decline, then rise again at about 800-1000%. The shape of the hump is generally similar to that for litter and soil respiration rates (Flanagan & Veum, this volume), except between 400 and 800% moisture, where there is a much greater decline in respiration rates than in weight loss rates, probably because leaching losses will be high at these moisture levels.
3. Levels of available calcium and phosphorus in the soil are both positively related to loss rates. The relationship appears to be logarithmic or asymptotic. Both of these nutrients interact with temperature and moisture, but it is not certain whether they interact with each other.
4. All the regression surfaces indicate a moisture optimum for decomposition near 400% of dry weight. At average tundra levels of phosphorus and calcium (60 ppm P and 1000-2000 ppm Ca), loss rates increase by about 20% per 1000° days above 0°C at optimum moisture levels. No similar statements can be made about phosphorus and calcium, as the exact form of the relationship between these, climate, and loss rates is still uncertain.
5. The relation of phosphorus and calcium to loss rates in these regressions is logarithmic or asymptotic in both cases, whereas there is a positive quadratic relationship of loss rates to Component IV of the P.C.A. We do not know why this is, but component IV also includes C/N ratio and pH, which may be having a significant effect on loss rates.

6. However, all these conclusions are based on correlative analyses and, though it seems likely that there are genuine causal relationships between loss rates and site condition, it is probable that some form of feedback system is working in at least some of the sites, whereby decay rates and site conditions are interdependent. This applies particularly to soil factors.

Additional data on first year litter losses

Table 3 lists weight losses from ten additional tundra sites, which were not included in the main analyses because sufficient site data were not available. Although detailed analyses are not possible, some general comparisons can be made. These data thus provide a useful check on the conclusions drawn from the main analyses.

These weight losses appear fairly typical of tundra sites, being largely in the range 0-40% loss in the first year, with Moss and Wood having lower losses than leaves and a few Soft leaves having losses greater than 50%.

From the limited site data available, it is possible to relate the sites in Table 3, approximately, to those included in the main analyses:

1. The Alaska/Yukon sites and the Harp shrub tundra sites are similar in vegetation and climate to the Kevo sites, and have similar loss rates.
2. Niwot Ridge is an alpine meadow. Climate and soil conditions were not available, but the weight losses appear comparable to those at other alpine meadow sites (e.g. Hardangervidda dry meadow), particularly when allowance is made for the state of the litter.
3. For Sivaya Maska, Petchora and Lammin-Suo, more detailed site data are available, but the loss rates shown are averages over all depths and subsites within these sites. However, subsite variation is small compared to the variation between these three sites, so these data are still useful for comparison between sites.

   Sivaya Maska has a Warm Continental climate, like that of the Kevo and Abisko sites, but the soils at Sivaya Maska are richer in nutrients, and loss rates are thus somewhat higher than for comparable sites at Kevo/Abisko. Although the losses given are for 9.5 months, the total first year loss is unlikely to be much higher, because of summer drought.

   Petchora (Gusinoe aapa-fen) is a eutrophic mire, similar to Hardangervidda in climate, but with much higher nutrient levels, and, as expected from these site conditions, loss rates are equal to or higher than those at the Hardangervidda meadows.

   Lammin-Suo is described as an "oligotrophic mire." The climate is Warm Oceanic, but colder than Moor House (mean annual air temperature 3.1°C). The vegetation is very similar to that at Moor House. Soil conditions are unknown, but probably also similar, and first year losses are almost identical to those at Moor House.
4. It is interesting to compare the decay rates of *Rubus* at these three sites (Sivaya Maska, Petchora and Lammin-Suo), and at Moor House and Abisko. They are all warm sites, so the main differences are between wet sites (Petchora, Moor House, Lammin-Suo) and dry sites (Abisko, Sivaya Maska), and between eutrophic (Petchora, Sivaya Maska) and oligotrophic (Abisko, Moor House, Lammin-Suo) sites. Comparison of the decay rates of *Rubus* at these sites yields the series wet eutrophic > dry eutrophic = wet oligotrophic > dry oligotrophic, which is the same pattern as derived from the main analyses.

Table 3. Additional weight loss results not included in the main comparative data set (Table 1) because of a lack of site data.

Site	Litter	Percentage loss 6 mo.	9 mo.	12 mo.	24 mo.	Comments and data sources
Dempster Highway, Yukon, Canada	Herbaceous litter		9.8	19.1		R. Wein (personal communica-
	Woody litter			13.4		tion)
Eagle Creek, Alaska, USA	Herbaceous litter		11.9	27.7		
	Woody litter		8.1	12.5		
Elliott, Alaska, USA	Herbaceous litter		10.3	21.0		
	Woody litter			13.4		
Niwot Ridge, USA (soil surface)	*Geum rossii*, leaves (green, dry)			43.4		Means from 5 vegetation noda:
	Salix planifolia, leaves (green, dry)			21.9		Recalculated from Webber (19
(30 cm)	*Geum rossii*, leaves (green, dry)			58.5		
	Salix planifolia, leaves (green, dry)			24.5		
Harp, USSR (moss shrub hummock tundra)	Range of site litter losses			13-27		Gortchakovsky & Andreyashki (1972)
(dwarf shrub moss spotty tundra)	Range of site litter losses			10-18		
(*Calamagrostis*-*Carex* swamp meadow)	Site rate by Jenny, Gessel & Bingham (1949) formula			24		
Sivaya Maska, USSR	*Betula nana*, green leaves		36.4			Means of 2 depths at 4 subsit
	Betula nana, yellow leaves		32.4			(9.5 months); M.S. Botch (per-
	Betula nana, twigs		6.3			sonal communication)
	Empetrum hermaphroditum		19.3			
	Rubus chamaemorus, leaves		35.6			
	Vaccinium spp., leaves and young stems		45.2			
	Pleurozium schreberi		8.0			
Petchora (Gusinoe appa-fen), USSR	*Sphagnum papillosum*			16.5	10.4	Means of 4 depths at 7 sub
	Sphagnum nemoreum			7.4	8.8	sites; M.S. Botch (personal
	Sphagnum fuscum			28.3	19.2	communication)
	Sphagnum magellanicum			25.8	24.9	
	Sphagnum majus			28.1	24.0	
	Chamaedaphne calyculata, leaves, stems, roots			19.1	23.3	
	Menyanthes trifoliata, leaves, stems, roots			75.9	79.5	
	Carex limosa, leaves, stems, roots			24.5	34.4	
	Rubus chamaemorus, leaves			57.0	63.2	
	Scheuzeria palustre, leaves, stems, roots			44.2	45.6	
	Betula nana, leaves			31.0		
	Betula nana, twigs			4.7		
	Eriophorum vaginatum, leaves			42.5		
Lammin-Suo (oligotrophic mire) USSR	*Eriophorum vaginatum*, leaves	19.8		23.7		Means of 3 depths at 4 sub
	Empetrum nigrum	12.7		22.0		sites; M.S. Botch (personal

Standing Dead and Below-Ground Remains

The available data on weight losses of standing dead (Table 4) and roots and underground stems (Table 5) are very sparse. No clear differences between sites are apparent, and the only conclusions that can be drawn are:

1. The losses from standing dead and below-ground parts are of the same order as those from litter of comparable quality.
2. The potential contribution of leaching to weight loss is indicated in the US data (Table 4) where the loss from unleached green leaves is much higher than that from leached leaves. Losses from the latter are similar to those from 1st and 2nd year standing dead.

DISCUSSION

Weight Loss and Decomposition

The results presented have been concerned with measurements of dry weight loss. This loss results from a combination of respiration, leaching and comminution losses, plus physical removal or addition of material (e.g. by fauna) and growth of microflora into, through and out of the sample. All these represent different paths and mechanisms of carbon transfer and cycling. We therefore need to examine the extent to which these processes contribute to the observed weight losses. Most of the evidence is circumstantial, but some broad conclusions can be inferred.

The high initial weight loss observed in most sites and litters probably results from a combination of leaching and microbial activity. The potentially leachable fraction of most plant remains is in the range 5-30% of dry weight, with lowest values in wood and highest in soft herbaceous leaves. This is also the fraction most easily utilised by microorganisms. Results from various studies (Nykvist, 1961; Bocock, Gilbert, Capstick, Twinn, Waid & Woodman, 1960; Flanagan, pers. comm.) show that leaching can remove most of this soluble fraction, but the leaching loss depends on the type of litter, its physical state (including wetness), the presence of aerobic or anaerobic conditions and the respiration rate. For individual litters, the change from aerobic to anaerobic conditions increases the leaching loss but lowers the respiration rate. These results, however, are from laboratory studies, and their relationship to field conditions is uncertain.

More direct estimates of the proportion of the total loss resulting from respiration are obtained by estimating weight loss from respiration data and comparing this with observed field weight losses in the same litter (Flanagan & Veum, this volume). The estimated weight loss due to respiration is generally about 50-100% of the observed weight loss, and the proportion of the observed weight loss accounted for by respiration seems to be negatively related to litter quality.

The action of fauna is probably a minor factor in most of the weight losses presented here, because 1) large litter-feeding fauna are absent or rare in tundra sites, and 2) colonisation and, presumably, comminution by small litter-feeding fauna (enchytraeids, tipulid larvae, micro-arthropods) increases as the litter decomposes. At Moor House, litter bags are 2-4 years old before 70% of them are colonised by enchytraeids (Latter, pers. comm.).

Assimilation by microflora, and growth of microflora into, through and out of the sample, may have considerable short-term effects on weight loss, even to the extent of producing significant weight gains (Kärenlampi, 1971). These do not usually persist

Table 4. Weight losses from standing dead plant remains. Losses at the Norwegian sites are measured by specific weight. Losses at Point Barrow and Eagle Summit are measured by litter bag.

Site	Subsite	Litter	% loss 3 mo.	 12 mo.	 15 mo.	 24 mo.	 36 mo.	Data source
Hardangervidda, Norway	Lichen heath	*Carex bigelowii* leaves		30		44	57	A.K. Veum (personal communication)
		Carex bigelowii leaves		34		74	88	T.V. Callaghan (personal communicati
	Wet meadow	*Carex nigra* leaves		28		43		A.K. Veum (personal communication)
		Eriophorum vaginatum leaves		27		43		
Point Barrow, USA	Site 2	*Eriophorum angustifolium* green leaves		28	32			P.W. Flanagan (personal communicatic
		Eriophorum angustifolium leached leaves	3	2	6	8		
		Eriophorum angustifolium 1 yr old leaves	6	6	8	10		
		Eriophorum angustifolium 2 yr old leaves	5	6	7	9		
		Carex aquatilis green leaves		26	35			
		Carex aquatilis leached leaves	3	2	3			
		Carex aquatilis 1 yr old leaves	5	5	6	7		
		Carex aquatilis 2 yr old leaves	5	4	7	10		
Eagle Summit, USA		*Dryas integrifolia* green leaves		23		29	36	
		Dryas integrifolia leached leaves	2	2	3			
		Dryas integrifolia 1 yr old leaves	8	8	10			
		Dryas integrifolia 2 yr old leaves	7	6	7			
		Dryas integrifolia 3 yr old leaves	4	5	5			
		Eriophorum vaginatum green leaves		25				
		Eriophorum vaginatum leached leaves	5	6	6			
		Eriophorum vaginatum 1 yr old leaves	4	5	6			
		Eriophorum vaginatum 2 yr old leaves	4	5	5			

Table 5. Weight losses from below-ground (B/G) plant remains. All losses are measured by litter bags except for *Carex bigelowii* at Hardangervidda Lichen heath, where losses were measured by specific weights.

Site	*Subsite*	*Litter*	*Weight loss (%)* ¾ yr	1 yr	2 yr	3 yr	4 yr	5 yr	*Data source*
Hardangervidda, Norway	Lichen heath	*Carex bigelowii* whole tiller (mainly rhizome)		20	28	40	50	60	T.V. Callaghan (personal communication)
	Wet meadow	*Carex nigra* roots	13	21					A.K. Veum (personal communication)
		Other roots	21	43					
Moor House, UK	Blanket bog	*Calluna* roots (surface)		5	11				O.W. Heal (see Fig. 1(d) and Fig. 2(a))
		Calluna B/G stems (surface)		7	10				
		Calluna B/G stems (1-5 cm)		6					
		Calluna B/G stems (6-10 cm)		6					
		Calluna B/G stems (11-15 cm)		4					
		Calluna B/G stems (16-20 cm)		4					
		Calluna B/G stems (>20 cm)		2					
		Eriophorum vaginatum roots (surface)		1	1				
		Eriophorum vaginatum roots (surface)		8					
		Eriophorum vaginatum roots (1-5 cm)		12					
		Eriophorum vaginatum roots (6-10 cm)		10					
		Eriophorum vaginatum roots (11-15 cm)		14					
		Eriophorum vaginatum roots (16-20 cm)		13					
		Eriophorum vaginatum roots (>20 cm)		19					

over longer periods, so that ingrowth is probably not an important phenomenon. However, microbial assimilation represents a carbon loss from the substrate which is not detected in measurements of weight loss. This will not, however, affect estimates of carbon loss from the ecosystem.

These fragments of evidence suggest that:

1. Respiration accounts for 50-100% of the total observed weight loss.
2. Leaching accounts for most or all of the remainder, especially in the earlier stages of decomposition.
3. Leaching may account for most of the total loss up to the stage of 20% weight loss in litters with high initial concentrations of soluble material.
4. In the later stages, comminution and removal by fauna may account for about 20% of the total loss.
5. Loss of material assimilated by microflora may be a significant loss from the substrate, which is not detected in weight loss measurements.

Organic Matter Accumulation and Turnover

The weight losses plotted in Fig. 1 approximate to a series of negative exponential curves, implying a constant fractional loss rate (g/g/unit time). Jenny, Gessel & Bingham (1949) have shown that if this loss rate is expressed as

$$k = \frac{\log_e \frac{(\text{wt. at start})}{(\text{wt. at time } t)}}{t} \qquad (1)$$

where t is in years, then, in a steady-state ecosystem, if I = total annual input of dead material and X_{ss} = total accumulated organic matter,

$$k = \frac{I}{X_{ss}} \qquad (2)$$

For a number of Tundra sites, both estimates of k have been calculated (Table 6). In nearly all cases, the value of k calculated from production and accumulation estimates is very much lower than that calculated from litter bag losses, especially in the warm bog sites. This difference can be caused by any or all of several factors:

1. Overestimation of litter bag losses. This is probably a relevant factor, since losses from the ecosystem are largely respiration losses, which tend to decline with increasing age of organic matter. Also, in litter bags, losses include leaching and comminution losses, which transfer material to other parts of the ecosystem, rather than out of the system.
2. Underestimation of production. This may also be a significant factor, though probably less so than 1.
3. Overestimation of accumulation. The errors in the measurements are unlikely to affect the result to any great extent.
4. Declining fractional loss rate. The decline in respiration with time has already been referred to. The graphs of weight loss against depth (Fig. 2) and the results from cellulose decomposition studies (Rosswall, this volume; Heal, Howson,

Table 6. Estimates of k from litter bag measurements (k_{LB}) and from measurements of primary production and organic matter accumulation (K_s) at some tundra sites. Estimates of k_{LB} are based on the lowest available litter bag losses.

Site	*Subsite*	*Total primary production (g/m^2)*	*Organic matter accumulated (kg/m^2)*	K_s	k_{LB}
Signy Island	*Chorisodontium*	480	46	0.0104	0.0101
	Drepanocladus ("dry")	632	2	0.2931	0.1508
	("wet")	709	3	0.2182	0.2744
Devon Island	Beach ridge	25	1	0.0250	
	Mesic meadow	375	35	0.0107	0.2232
Barrow	Site 2	c.250	51	0.0050	0.0600
Abisko	Stordalen mire	c.150	100	0.0015	0.0513
Hardangervidda	Lichen heath	285	11	0.0265	0.0513
	Dry meadow	533	31	0.0172	0.0513
	Wet meadow	665	57	0.0116	0.0305
	Birch forest	780	22	0.0355	0.3853
Moor House	Blanket fog	c.650	200	0.0033	0.0726
Glenamoy	Bog	c.400	400	0.0010	0.1054

French & Jeffers, this volume) indicate that decay rates may also decline with depth, particularly in waterlogged soils in the warmer sites. In the two sites where k_{LB} is less than or equals K_s, there is no measurable decline with depth.

5. Major environmental changes during the period of accumulation. Pollen analyses in peaty sites may reveal these, where relevant.
6. The system may not be in steady-state.

Some of the above possibilities can be tested by means of constant-coefficient models of production, decay and accumulation. These have been produced for the peat sites at Moor House and Glenamoy (Clymo, in press; Jones & Gore, in press; O'Connel, 1971). Clymo's model has also been run for the Abisko site. Each of these is based on the basic steady-state equation:

$$\frac{dx}{dt} = I - kx \tag{3}$$

where I = organic matter input (production)
x = organic matter accumulated
t = time
k = the decay constant in eq 1 and 2 above.

In all of them, if the value of k derived from litter bag studies is used without modification, then the amount of peat accumulated is drastically underestimated. In all these models, the decline in decay rates with depth was the most critical factor, but they are all for very waterlogged sites, and other factors may be important in other kinds of sites. The Moor House models indicate that most of the other factors listed

have some effect, even though the decline with depth is the main one.

These observations indicate the limitations of weight loss studies in the estimation of long-term decay rates, the need for studies on the later stages of decomposition and for quantitative studies on the circulation and transfer of material within the decomposer subsystem.

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